

## Range Expansion of the Eastern Fox Squirrel within the Greater Los Angeles Metropolitan Area (2005 – 2014) and Projections for Continued Range Expansion

Rosemary B. Garcia<sup>1</sup> and Alan E. Muchlinski<sup>2</sup>

<sup>1</sup>*Department of Geosciences and Environment, California State University, Los Angeles, Los Angeles, CA 90032*

<sup>2</sup>*Department of Biological Sciences, California State University, Los Angeles, Los Angeles, CA 90032*

**Abstract.**—Monitoring the spread and distribution of introduced species in an area can be challenging due to a variety of issues. Range expansion may exceed expected rates if the area of introduction is more suitable than expected, and may be slowed by an area in which it is difficult to establish a population. The species of interest in this study is the Eastern Fox Squirrel (*Sciurus niger rufiventer*) and the focus of the study is the spread of the species in Southern California. Previous studies have shown a steady and continuous spread from main points of introduction in Southern California and the species is now considered well established in the region. In this study, we collected and mapped new location data within Southern California. We discuss the spread of the Eastern Fox Squirrel in this area from 2005 through 2014 and include habitat suitability models to project the potential future distribution of the species. Results show that the Eastern Fox Squirrel has spread east into Rancho Cucamonga, into southern portions of Irvine, and has maintained isolated populations in places such as San Diego and Riverside. Our models suggest potential future paths of movement for contiguous range expansion.

---

The goals of this study were to (1) document range expansion of the Eastern Fox Squirrel (*Sciurus niger* – hereafter EFS) within the greater Los Angeles metropolitan area over the time period of 2005 – 2014, and (2) use an ecological niche model to project potential future range expansion of the species in Southern California. King et al. (2010) described the range of the EFS in Southern California as of 2004 with general information on range expansion from the time of introduction to Los Angeles in 1904 through 2004. Range expansion of the EFS over the 100-year period occurred through natural dispersal of animals and through human activity. Natural dispersal of animals would elicit a contiguous mode of range expansion that depended mostly on the rate of dispersal and the presence of available habitat. Range expansion due to human activity could produce a noncontiguous type of range expansion through live trapping and relocation some distance away from the leading edge of natural range expansion. King et al. (2010) found that through human activity, isolated pockets of animals appear where the species did not previously occur. These isolated pockets of animals would be absorbed into the metapopulation as years pass and range expansion through natural dispersal meets the isolated pockets of animals.

Mammals that are introduced to a particular location may, over time, spread out from the original place of introduction. Range expansion may continue as long as there is suitable available contiguous habitat, biotic factors such as competition with native species are not a limiting factor, and physical factors such as temperature or elevation do not make an area unsuitable for habitation, as found by Geluso (2004) and Goheen et al. (2003) for tree squirrels.

An invasive species such as the EFS provides a good model for looking at factors that influence range expansion of small mammals in a large metropolitan area, and at the rate of range expansion. King et al. (2010) and Koprowski (1994) found that the EFS has been introduced to many areas outside of its natural range, and within California it is strongly, though not exclusively, associated with human habitation and development – thereby providing copious data for analysis.

Another example of range expansion showing both contiguous and noncontiguous modes has been provided for the Eastern Gray Squirrel (*Sciurus carolinensis*, hereafter known as EGS) in the United Kingdom (Bertolino et al. 2008). The EGS was first introduced to the United Kingdom in the 1870's and soon after spread to parts of England, Wales and Scotland (Parsons 1937). While contiguous range expansion through natural dispersal was first evident in southern England, non-contiguous range expansion through human activity likely produced isolated pockets of animals in the middle and northern section of the United Kingdom as well as in Ireland (Teanga 2000).

While it is possible to describe range expansion of the EFS within the greater Los Angeles metropolitan area in fairly accurate detail, it is also possible to utilize ecological niche modeling software such as Maxent (Phillips et al. 2004, 2006) to make projections related to potential future range expansion of the EFS in Southern California. Cooper and Muchlinski (2015) suggested that lowland populations of the Western Gray Squirrel (WGS) occupy fragments of habitat which the EFS may occupy as range expansion continues. These lowland populations were at altitudes up to ~450 m elevation. Muchlinski et al. (2009) and Cooper and Muchlinski (2015) suggested that since the EFS has been documented to replace the WGS in some habitats where the two coexist, it is expected that additional lowland populations of the WGS residing in the greater Los Angeles metropolitan area and Southern California will be extirpated over time. At this point in time it is not possible to know if or how the EFS will impact populations of the WGS if the range of the EFS expands to habitats at higher elevations.

Range expansion of the EFS in the Los Angeles metropolitan area over the 10-year period between 2005 and 2014 occurred mainly on the eastern and southeastern fronts of range expansion. Therefore, these two fronts of range expansion, as well as projections for potential future range expansion, are the focus of this study.

## Materials and Methods

The baseline data set used in this study for monitoring range expansion (995 location points) was published by King (2004) and later by King et al. (2010). King (2004) utilized a citizen science approach along with information from several wildlife care centers to collect data on present (2003–2004) and historical sightings of the EFS. For the current study, location data from throughout California were gathered over the time frame of January 2005 through December 2014. Of the 1376 location points obtained for the area from Santa Barbara south to San Diego between 2005 and 2014, 48.3% of the location points came from wildlife rehabilitation centers, 24.7% came from online geodatabases such as the Global Biodiversity Information Facility (GBIF) and 26.8% came from AEM and several former graduate students trained in the identification of the EFS. Data obtained through the GBIF included research-grade observations submitted through various iNaturalist pages. Sources of all observations are shown in Table 1. Since the EGS is not present within Southern California, confusion of the EFS with the EGS was not an issue in species identification for this paper. Calculation of the rate of range expansion over the time period of 2005-2014 followed previously established methods from King et al (2010).

Table 1. Location sources for observations of the Eastern Fox Squirrel, *Sciurus niger* within Southern California from 2005 through 2014.

Data Source	Number of Location Points
California Wildlife Center	136
California Tree Squirrels	137
Alan Muchlinski and Students	233
Global Biodiversity Information Facility	341
Orange County Vector Control	45
Squirrelmender Wildlife Rehabilitation	34
Wetlands & Wildlife Care Center	171
California Department of Public Health	279
Total	1376

An ecological niche model for the EFS in Southern California area was created using the Maxent software program, a maximum entropy approach for modeling species habitat as described by Phillips et al. (2004, 2006) and Elith (2014). Merow et al. (2013) suggest that Maxent is the most widely used species distribution/environmental niche modeling software because it typically outperforms other programs based on the accuracy of the predictions from the model. Also, machine learning models such as Maxent, when used in the default mode, are less affected by highly correlated variables than traditional statistical models (Phillips et al. 2006; Elith et al. 2011). A process called regularization helps prevent overfitting of the model (Merow et al. 2013). The Maxent program has been used in ecological niche modeling for a large number of species, as seen in Phillips and Dudik (2008) and Kebede et al. (2014).

The Maxent program takes presence-only data, fits those data to a set of selected abiotic and biotic environmental predictors, and projects to other locations where the selected set of environmental predictors match in varying degrees the predictors where the species does exist. General biotic and abiotic factors used in our model are outlined in Table 2. Variables used from BIOCLIM<sup>1</sup> included bio 1 through bio 19, which represent annual trends for certain environmental variables, monthly trends on temperature and precipitation, as well as altitude. The remaining variables related to land development, land cover type, and tree canopy cover (Table 2) were obtained from the United States Geological Survey (USGS).

Location addresses for observations were converted to geographic coordinates by finding the latitude and longitude coordinates of each individual sighting through Google Maps. The coordinates were saved as a text file along with corresponding information related to species type, year, specific date seen if given, and additional information if given. The accuracy of location data varied by source, being between 3 to 10 m for data obtained using GPS location applications and between 15 to 30 m using street address locations on Google Maps. The accuracy of the location data is within the accuracy level of the environmental variables from BIOCLIM, which is 1 km<sup>2</sup>.

The machine learning methodology of Maxent makes the algorithm highly accurate in a predictive manner but more difficult to interpret in terms of highly rated variables than traditional methods because the method creates non-linear functions (Elith 2014). Maximum entropy models such as Maxent initially assume a uniform distribution for the species, then apply iteratively adjusted constraints to estimate the actual species distribution (Elith et al. 2011;

<sup>1</sup><http://www.worldclim.org>



Table 2. Biotic and abiotic variables used in the Maxent model for future range expansion by the Eastern Fox Squirrel, *Sciurus niger*, in Southern California.

Variable	Description	Unit	Source
Climate	Variables bio 1 through bio 19; Annual trends, seasonality and extreme or limiting environmental factors	Varies	BIOCLIM
Temperature	Average monthly mean, minimum and maximum temperatures	(°C)	BIOCLIM
Precipitation	Average Monthly Precipitation	millimeters	BIOCLIM
Altitude	Elevation above sea level	meters	BIOCLIM
Impervious Surfaces	Percent of developed impervious land (paved surfaces)	Percent	USGS
Landcover Type	Categorical Description of Landcover	Categorical	USGS
Tree Canopy	Area or proportion of cell covered by tree canopy	Percent	USGS

Phillips et al. 2006). The output of Maxent is a relative probability distribution that sums to one. It provides the relative probability of each cell containing suitable habitat, in comparison to the other cells in the raster (Merow et al. 2013). The constraints are set up across environmental covariates, instead of across geographic space, then applied to the geographic space. Maxent applies the constraints, but maintains the most uniform distribution possible. Maxent randomly changes the coefficients for each predictor, or environmental variable, and accepts the variable if it increases the gain, or the deviance from the original maximum entropy model.

The pre-established environmental variables from BIOCLIM and the USGS (Table 2) were added for the analysis. These variables correspond with biotic and abiotic factors that would most likely represent where a species would be found. Fifteen replicates were done with data divided 75% for training the model and 25% for testing the model within each replicate. The maximum number of iterations within a replicate run was set at 5000 to allow enough iterations for convergence of a model.

The Random Seeding Option was utilized so that the first iteration within a replicate run would begin at a random data point within the training data set. Replicate Run Type was set to subsample so that data points were randomly split into 75% training and 25% testing subsets for each replicate. Subsampling is one form of cross-validation available within Maxent. Receiver Operating Characteristic (ROC) plots with average Area under the Curve (AUC) values were generated across the 15 replicate models. The summary response curve includes the mean AUC value  $\pm$  one standard deviation error bars (Phillips et al. 2006; Phillips and Dudik 2008).

The resulting average model from all trials was creating as a logistic output and imported into ArcMap for reclassification. The suitability classifications were made with Jenks Natural Breaks (Jenks 1967) which determines the best arrangement of values into classes. Habitat classifications used were Not Suitable, Low Suitability, Medium Suitability, High Suitability and Very High Suitability, which are relative and not absolute. In a binary output, all locations that are not classified as Not Suitable Habitat are considered to represent Suitable Habitat. Jenks Natural Breaks provides a division of habitat suitability according to natural grouping of values from the logistic output of the model, which although not absolute, does provide additional information about the habitats classified as suitable. Location sightings of the squirrels were added to the resulting maps.

The two maps showing the habitat suitability models represent what we refer to as minimum and maximum potential suitable habitat for the EFS in Southern California. The minimum



model was generated by using 1390 location points of the EFS from within Southern California (Santa Barbara to San Diego) over the time period of 2004 – 2015. The maximum model was generated by using a total of 5699 location points: 5475 from within the entire State of California + 224 from the native range of *S. niger rufiventer* over the same time period. We used location data for *S. niger rufiventer* from states where *rufiventer* is the only subspecies present within the state (Koprowski 1994). Lance et al. (2003) and Claytor et al. (2015) suggested that the subspecies *S. niger rufiventer* is the main subspecies present within California, and information on habitat suitability from the native range could be important in projecting potential future range expansion within California. The data from other states include the broader environmental conditions that the EFS tolerates rather than the more limited conditions currently encountered solely within Southern California. The maximum model could be more representative of the species' actual tolerance ranges, and therefore may better represent areas the species could colonize within Southern California. However, the exact accuracy of the models can only be determined by future studies that assess the presence of the EFS within various areas in the future. Since the dataset used for this study is available via a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License, we encourage researchers who are conversant with other ecological niche modeling programs to further investigate these data. Those individuals who submitted observations to iNaturalist are recognized in the data set.

A Maxent model can be evaluated by looking at how well it explains training data and how it predicts data from another data set. It is a common practice to randomly set aside a portion of the original data set for testing the model once it has been trained (Baldwin 2009). However, in presence only modeling test data are likely to have the same biases in geographic and environmental space as the training data. Therefore, test data may not provide a perfect test of accuracy in predicting species distributions.

To determine goodness of fit for the two models with test data we examined the model's discriminatory ability by measuring the AUC of the ROC plot (Baldwin 2009). The greater the area under the curve, the higher the predictive ability of the model, and the better fit it is to the data used to build the model. AUC values for the ROC plot can range from 0.5 to 1.0. A value of 0.5 indicates a fit of observation data (true positives plotted against false positives) no better than random, and a value of 1.0 indicates a perfect fit of observation data to the model (Baldwin 2009). The AUC is not a perfect objective measure of the predictive power of the model but few alternatives are available for presence only data since absences have not been tested (Merow et al. 2013). AUC is rank-based so models can only be compared using the AUC if they were built for the same landscape, used the same background sample, and tested the same species with the same test data (Elith et al. 2011).

## Results

The overall distribution of the EFS within the Los Angeles metropolitan area as of the end of 2014 is shown in Fig. 1. Shown in Fig. 2 are the range expansion fronts from 2004 and 2014 in the eastern and southeastern portions of the Los Angeles metropolitan area. The EFS now occupies areas to the east and south of the eastern front of range expansion in 2004, which was located at the western edge of the City of Claremont, including the Cities of Pomona, Claremont, Montclair, Upland, Ontario, and Rancho Cucamonga. Current borders of contiguous range expansion as of 2014 (Fig. 2) appear to be near Interstate Highway 15 which runs along the eastern edge of the Cities of Rancho Cucamonga and Ontario, and near California Highway 60 which runs along the southern edge of the Cities of Pomona, Montclair, and Ontario (Fig. 2).

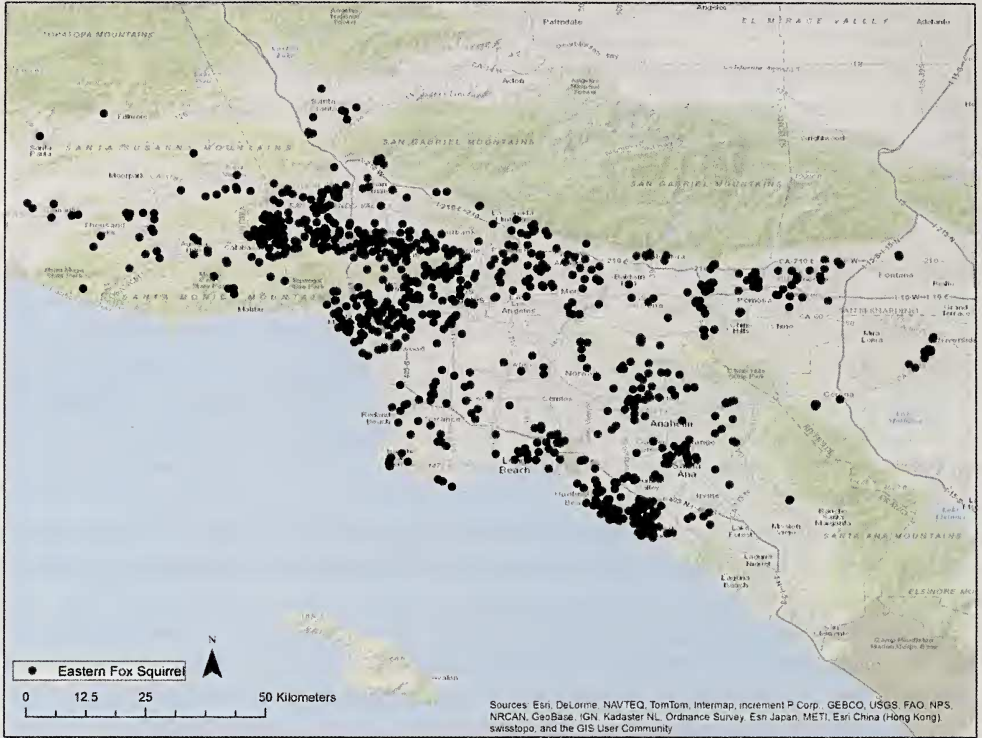


Fig. 1. Distribution of the Eastern Fox Squirrel (*Sciurus niger*) in the greater Los Angeles metropolitan area as of 2014.

The current boundaries on the expanding eastern front are the foothills of the San Gabriel Mountains to the north, Interstate Highway 15 to the east, and California Highway 60 to the south. Although animals have been sighted by AEM on property of Sierra Lakes Golf Club in the City of Fontana, it is very likely the presence of animals on the golf course is the result of human activity as the golf course is ~ 3.5 km east of Interstate Highway 15 and ~ 10 km east of the front of contiguous expansion range. The total linear distance of contiguous range expansion from the eastern most location observed in 2004 to the eastern-most location observed in 2014 (10 yrs.) was 15 km, giving a contiguous range expansion rate of 1.50 km/year.

We do not have reports of the EFS in the Chino Valley south of California Highway 60, east of Highway 71, and west of Interstate Highway 15. Therefore, the EFS appears to be absent, as of 2014, from the Cities of Chino and Chino Hills, including the heavily wooded flood plain behind Prado Dam at the junction of Highway 71 and Interstate Highway 91.

The current distribution of the EFS in the southeast Los Angeles metropolitan area runs through the Cities of Diamond Bar, Brea, Yorba Linda, Anaheim, Orange, Tustin, Santa Ana, Garden Grove, Westminster, Fountain Valley, Huntington Beach, Costa Mesa, and Irvine. The front of contiguous range expansion in the southeastern direction appears to be along the southeastern boarder of the City of Irvine (Fig. 2), where additional residential development is occurring at this time. Contiguous range expansion to the east of the City of Diamond Bar appears to have been halted by an area of open, mostly tree-less land that runs from Highway 60 in the north to the San Juan Hills in the south. This area of open space currently separates







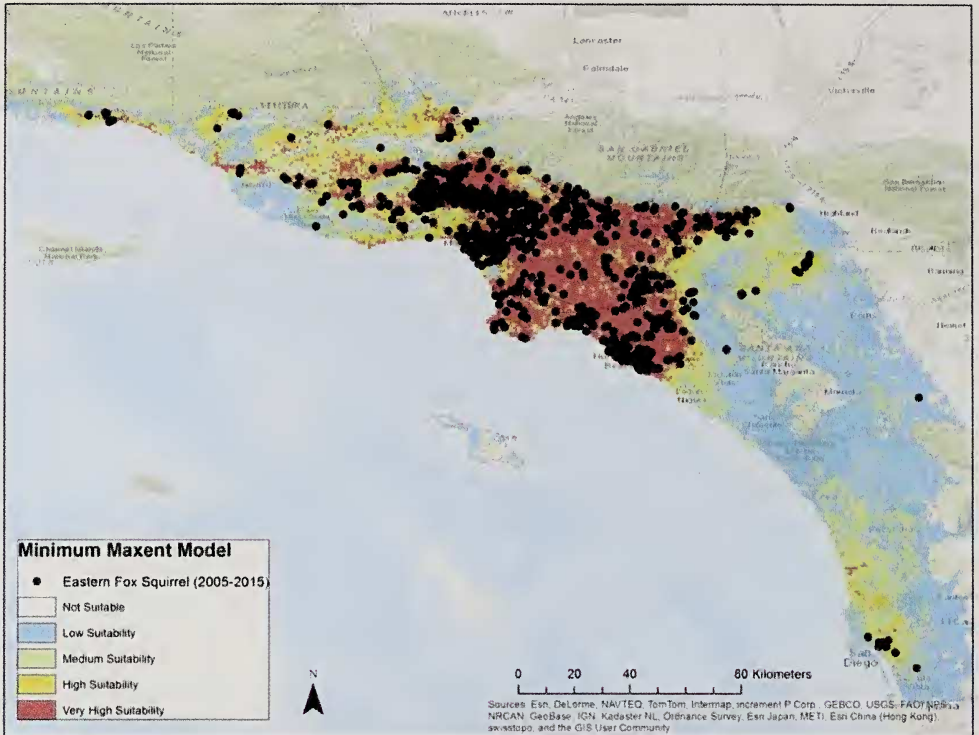


Fig. 3. A minimum habitat suitability map developed for the Eastern Fox Squirrel (*Sciurus niger*) using the Maxent software program. Location data along with abiotic and biotic variables for this model included data only from Southern California over the time period of 2004 through 2015.

Riverside. Arrival of the EFS in the City of Corona has occurred within our 10-year study period but the population in Riverside has been present in the Wood Streets Area of Riverside for at least 40 to 50 years (Gilbert Garcia, former Wood Streets Resident, Personal Communication) (Fig. 2). The presence of the isolated population in Riverside was not captured in the study conducted in 2004 and expansion of this population in terms of geographic area seems to have been limited.

The minimum projection for potential range expansion by the EFS within Southern California is shown in Fig. 3. Since the Maxent model is based upon presence only data, with extrapolation to habitats that share to varying degrees the abiotic and biotic characteristics similar to habitats where the species has been observed within California, areas where the EFS has been observed are shown in bright red. Areas in white would be considered unsuitable habitat based upon the variables used in the model. Moving from a brighter to a cooler shade of color would indicate a reduction in the potential of the habitat being suitable for the EFS, based upon location and environmental data only from within Southern California.

Based upon the minimum model, most of the area between the leading edge of contiguous range expansion from 2014 to the isolated populations in Fontana, Riverside, Corona, and Foothill Ranch appears to be suitable habitat for the EFS. Therefore, over time, we would expect developed areas south of Interstate Highways 210, 10, and 60, and north of Interstate Highway 91 to be populated with EFSs. We would also expect range expansion southeast of the City of Irvine along the Interstate Highway 5 corridor to the City of San Clemente.

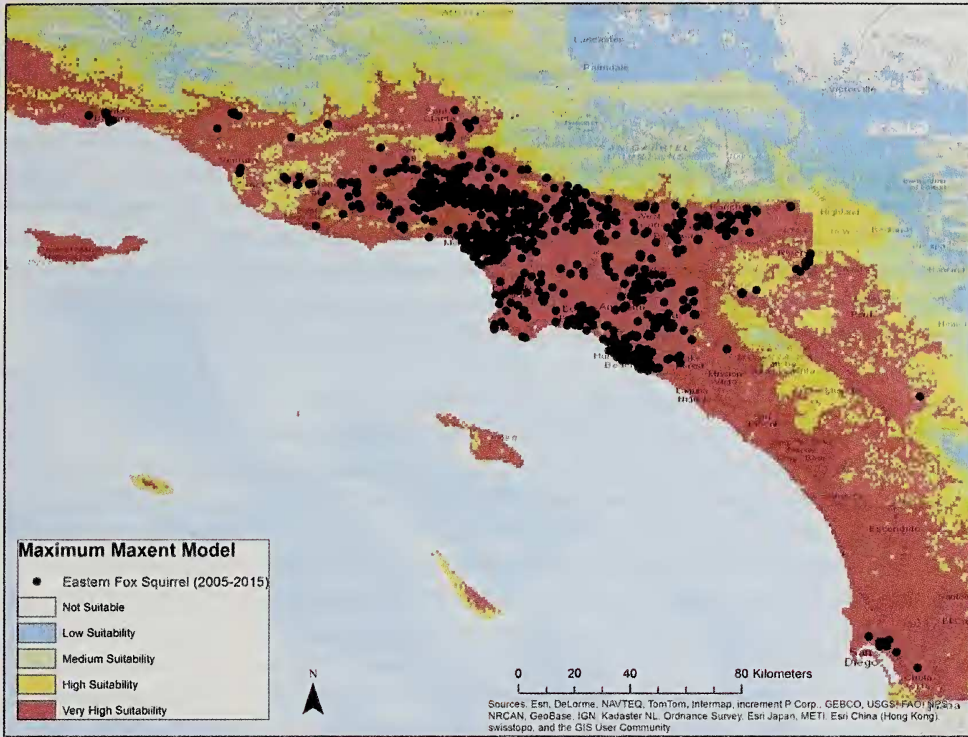


Fig. 4. A maximum habitat suitability map developed for the Eastern Fox Squirrel (*Sciurus niger*) using the Maxent software program. Location data along with abiotic and biotic variables for this model included data from within the entire State of California along with data from others states over the time period of 2004 through 2015 where the subspecies *Sciurus niger rufiventer* is the only subspecies found in that state.

According to the minimum model the Camp Pendleton Marine Base may serve as a low suitability habitat providing a break between suitable habitat around San Clemente and suitable habitat to the south beginning near Carlsbad. A large amount of suitable but currently unoccupied habitat exists within San Diego County between and along the Interstate 5 and Interstate 15 corridors.

The maximum projection for potential range expansion by the EFS within Southern California is shown in Fig. 4. Regions where the maximum model projects an increase in very high suitability to high suitability habitat include (1) the area from the current front of range expansion in Orange and San Bernardino Counties a little further to the east and then southeast to San Diego, including the coastal Interstate 5 and inland Interstate 15 corridors, along with the coastal mountains between the two corridors, and the Santa Ana Mountain Range; (2) the Santa Monica Mountains and areas to the north and northwest of the this mountain range; and (3) the Santa Ynez Mountains north of Santa Barbara. The vast majority of habitat in these areas is at an elevation below 1000 m with some habitat in the Santa Ynez Mountains extending up to 1400 m. An increase in medium to low suitability habitat is observed in the Tehachapi Mountains, in the high desert areas around Palmdale, Lancaster and Littlerock eastward to developed areas around Victorville, Hesperia, and Apple Valley, which are at elevations near or below 1000 m.

Range expansion by the EFS into urbanized areas within deserts is certainly possible based upon the presence of the EFS within residential areas of Yuma, Arizona, along with their presence



in some agricultural areas across the Colorado River inside of California (Jack Crayon, California Department of Fish and Wildlife, Personal Communication). Potential range expansion of the EFS into desert regions that are associated with human habitation seems to mark a significant departure from the native habitat of the species.

The goodness of fit of test data for our maximum Maxent model is indicated by an AUC value of 0.918  $\pm$  0.002SD for the Maxent ROC plot. The AUC value of the model using test data only from Southern California is 0.966  $\pm$  0.003SD. Since the two models were generated from different data sets we cannot say that the model with the higher AUC value represents a better model than the model with the lower AUC value. However, the high AUC values for both models indicate a very good fit of the data used to generate each model. The low values of the standard deviations also indicate a tight fit of the data to each model.

### Discussion and Conclusions

The introduction and spread of non-native invasive species through a previously uninhabited area tends to follow a general process. The initial arrival, which can be by human introduction, introduces the species to the general area. Afterwards, the species establishes its place in the local niche. This is the ideal time to control and eradicate the species before it becomes impractical to contain. If the species is not contained by this time, then the invasive species will begin to displace native species, and the focus shifts from eradication of the invasive to mitigating damage caused to the native species. If nothing can be done to contain the invasive species at this time, then the invasive species dominates the ecosystem, and land managers can only try to maintain the current state of invasive and native species at that point (CDFW 2015).

Geography is also an important contributor to the current spread and range of the invasive species. For the EFS, knowing the geography of the area that the species is currently present in and has been present in can be extremely important for population control. The EFS has expanded its geographic range within the greater Los Angeles metropolitan area over the 10 yrs. of this study and continued range expansion in the northwest, east, and southeast directions is highly probable. King et al. (2010) estimated range expansion rates from 0.44 to 3.44 km/yr. based upon historical records. Our study provided contiguous range expansion rate estimates of 1.50 to 3.00 km/yr. and are probably a more realistic estimate of the contiguous range expansion rate through highly suitable suburban habitat.

Not all areas of suitable habitat behind the front of contiguous range expansion are occupied immediately by the EFS. Abiotic factors such as the presence of freeways or the presence of large industrial areas, and biotic factors such as the absence of adequate tree coverage can leave pockets of habitat which are not immediately occupied by the EFS. Frank G. Bonelli Regional Park in the City of San Dimas is an example where the presence of a freeway may have locally stopped animals from continued eastward dispersal. While the EFS was present in surrounding cities such as LaVerne, Claremont, and Montclair by 2004, the species did not enter the northern section of Bonelli Park until 2010 and the southern section of the park until 2012 (AEM). The first animals observed in the southern section of the park were most likely relocated by humans from the western, residential side to the eastern, park side of Interstate Highway 57. Animals could have entered the northern section of the park by dispersing south from previously occupied areas.

In many regions of Southern California, the higher elevation oak/conifer forests are separated from areas where EFSs currently reside by a zone of chaparral vegetation which is not suitable for habitation by tree squirrels. The zone of chaparral vegetation may act as a barrier to direct dispersal of the EFS to the oak/conifer forests above 1000 m elevation. Therefore, appearance



of the EFS in high elevation oak/conifer forests in southern California would most likely be a sign of human-assisted dispersal to those areas.

A major issue to address is what may happen if the EFS is introduced to higher elevations of the local mountain ranges. By adding environmental data to the ecological niche model from observations of the subspecies *Sciurus niger rufiventer* found within the native range, there appears to be a slight increase in suitable habitat within the higher elevation mountain ranges. However, elevations above 1000 m do not generally appear as suitable habitat with the maximum model. The highest elevation within the Santa Monica Mountains is approximately 1000 m and the maximum model describes this area as highly suitable habitat for the EFS. Several peaks within the Santa Ana Mountain Range are above 1000 m elevation but many areas are below the 1000 m level. Habitat within certain higher elevation areas of the San Bernardino Mountains, especially around the cities of Big Bear, Forest Falls, Lake Arrowhead, and Lake Gregory is highly fragmented due to human habitation. Also, ground cover within the coniferous forest around these areas of human habitation is minimal, a situation which is very conducive to the EFS (Gatza 2011). Even though the maximum model does not describe the higher elevations of the San Bernardino Mountain Range as suitable habitat, vigilance for human initiated introductions should be maintained.

The Santa Monica Mountains have an abundance of oak trees which have supported significant populations of the WGS. As pointed out by Erkebaeva (2013), replacement of the WGS by the EFS occurs faster in oak woodlands than in mixed oak/conifer woodlands below 1000 m. Significant residential development with associated habitat fragmentation is also found within the Santa Monica Mountains. Habitat suitability models have shown that the species of trees in an area, particularly a low to medium percentage of oak trees and medium to high percentage of conifers, have a positive relationship with the relative abundance of the WGS (Erkebaeva 2013).

In terms of preserving the WGS in Southern California, a focus could be placed on the conservation of natural areas and limitation of habitat fragmentation. Proper control methods can help reduce the rate at which invasive species such as the EFS can expand. A related issue is potential relocation through human activity of the EFS to areas in the San Gabriel and San Bernardino Mountain Ranges. These areas can be kept as exclusive WGS habitat if the presence of the EFS is caught early after an initial introduction and mitigation measures are activated. However, it is often difficult to track releases and determine the extent of a new population until it is already firmly established.

Maintaining local native vegetation and controlling invasive populations is important in controlling the rate at which the EFS can establish itself in an environment. With continued decadal surveys, trends can be found over time to determine if there are more specific patterns that can affect the distribution of both the EFS and the WGS. For now, a watchful eye on both species and proper management will help to keep the EFS in controlled populations and the WGS in viable populations.

#### Acknowledgements

We thank the California Department of Public Health West Nile Virus Surveillance Program, especially Leslie Foss, Vicki Kramer, and Kerry Padgett. Ruby Alvidrez, Carly Creley, Lauren Zameito, Gina Navia, and Christopher DeMarco were students who contributed observations. The following wildlife rehabilitation centers provided data used in this study: California Living Museum, California Wildlife Center, Critter Creek Wildlife Station, Gold Country Wildlife Rescue, Lindsey Wildlife Museum, Peninsula Humane Society, SPCA Monterey County, Sonoma County Wildlife Rescue, Squirrelmender Wildlife Rehabilitation, Stanislaus Wildlife

Rehabilitation Center, Suisun Wildlife Rescue Center, Sulphur Creek Nature Center, Wetlands and Wildlife Care Center, WildCare, and Wildlife Center Silicon Valley. We also thank the many individuals who utilized iNaturalist or other sources to submit observations of the EFS within California and other states. Recognition of individuals is available through the GBIF ID Number for each observation contained within the dataset. We thank the three anonymous reviewers who provided constructive comments to improve this manuscript. Maps were created using ArcGIS<sup>®</sup> software by Esri. ArcGIS<sup>®</sup> and ArcMap<sup>™</sup> are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. The DOI's for the data used to generate the Minimum Maxent Model and Maximum Maxent Model are 10.13140/RG.2.2.13672.06407 and 10.13140/RG.2.2.20382.95043, respectively.

### Literature Cited

- Baldwin, R.A. 2009. Use of maximum entropy modeling in wildlife research. *Entropy* 11:854–866.
- Bertolino, S., P.W.W Lurz and S. Rushton 2008. Predicting the spread of the American grey squirrel (*Sciurus carolinensis*) in Europe: A call for a co-ordinated European approach. *Biol Conserv.* 141: 2564–2575.
- [CDFW] California Department of Fish and Wildlife. 2015. About invasive species in California. Retrieved from <https://www.wildlife.ca.gov/Conservation/Invasives/About>
- Clayton, S.C., A.E. Muchlinski and E. Torres 2015. Multiple introductions of the eastern fox squirrel (*Sciurus niger*) in California. *Mitochondria DNA* 26:583–592.
- Cooper, D.S. and A.E. Muchlinski 2015. Recent decline of lowland populations of the Western Gray Squirrel in the Los Angeles area of Southern California. *Bull. So. Calif. Acad. Sci.* 114:42–53.
- Elith, J. 2014. Predicting distributions of invasive species. arXiv:1312.0851 [q-bio.PE]. in press.
- Elith, J., S.J. Phillips, T. Hastie, M. Dudrák, Y.E. Chee and C.J. Yates 2011. A statistical explanation of maxent for ecologists. *Diversity and Distributions* 17:43–57.
- Erkebaeva, K. 2013. Habitat structure and extinction risk modeling of *Sciurus griseus* in long-term coexistence habitats of southern California. Master's thesis. California State University, Los Angeles. Los Angeles.
- Gatza, B.P. 2011. The effects of habitat structure on western gray squirrels and invasive eastern fox squirrels. M.S. thesis, California State Univ., Los Angeles.
- Geluso, K. 2004. Westward expansion of the eastern fox squirrel (*Sciurus niger*) in northeastern New Mexico and southeastern Colorado. *Southwestern Nat.* 49: 111–115.
- Goheen, J.R., R.K. Swihart and J. Robins. 2003. The anatomy of a range expansion: latitudinal changes in foraging behavior and cranial morphology of North American red squirrels. *Oikos* 102:33–44.
- Jenks, G.F. 1967. The data model concept in statistical mapping. *International Yearbook of Cartography* 7:186–190.
- Kebede, F.P., D. Moehlman, A. Bekele and P.H. Evangelista. 2014. Predicting seasonal habitat suitability for the critically endangered African wild ass in the Danakil, Ethiopia. *Afr. J. Ecol.* 52:533–542.
- King, J.L. 2004. The current distribution of the introduced fox squirrel (*Sciurus niger*) in the greater Los Angeles metropolitan area and its behavioral interaction with the native western gray squirrel (*Sciurus griseus*). M.S. Thesis, California State University. Los Angeles.
- King, J.L., M.C. Sue and A.E. Muchlinski. 2010. Distribution of the eastern fox squirrel (*Sciurus niger*) in Southern California. *Southwest Nat.* 55:42–49.
- Koprowski, J.L. 1994. *Sciurus niger*. *Mammalian Species*. 1994: No. 479.
- Lance, S.L., J.E. Maldonado, C.I. Bocetti, O.H. Pattee, J.D. Ballou and R.C. Fleischer. 2003. Genetic variation in natural and translocated populations of the endangered Delmarva fox squirrel (*Sciurus niger cinereus*). *Conserv. Genet.* 4(6):707–718.
- Merow, C., M.J. Smith and J.A. Silander Jr. 2013. A practical guide to Maxent for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*. 36:1058–1069.
- Muchlinski, A.E., G.R. Stewart, J.L. King and S.A. Lewis. 2009. Documentation of replacement of native western gray squirrels by introduced eastern fox squirrels. *Bull. So. Calif Acad. Sci.* 108:160–162.
- Parsons, B.T. and A.D. Middleton. 1937. The distribution of the grey squirrel (*Sciurus carolinensis*) in Great Britain in 1937. *J. Anim. Ecol.* 6:286–290.
- Phillips, S.J., M. Dudík and R.E. Schapire 2004. A maximum entropy approach to species distribution modeling. *Proceedings of the Twenty-First International Conference on Machine Learning*, pp. 655–662.

- Phillips, S.J., R.P. Anderson and R.E. Schapire 2006. Maximum entropy modeling of species geographic distributions. *Ecol Model.* 190:231–259.
- Phillips S.J. and M. Dudík 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31:161–175.
- Teangana, D.Ó, S. Reilly, W.I. Montgomery and J. Rochford 2000. Distribution and status of the Red Squirrel (*Sciurus vulgaris*) and Grey Squirrel (*Sciurus carolinensis*) in Ireland. *Mammal Rev.* 30:45–56.